

# THE INTERACTION OF PRESCRIBED BURNING AND SITE CHARACTERISTICS ON THE DIVERSITY AND COMPOSITION OF A GRASSLAND COMMUNITY ON SANTA CRUZ ISLAND, CALIFORNIA

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## ABSTRACT

During the last 2 centuries, grasslands in California have undergone dramatic changes as community composition has been severely altered, leading to a conversion from communities dominated by native perennial bunchgrasses and forbs to communities comprising predominantly nonnative annual grasses and forbs. A series of 3 prescribed burns was done in grasslands on Santa Cruz Island, California, between 1993 and 1995. The 2 main goals of the burns were to (1) begin an evaluation of the effect of fire as an ecological process in the islands vegetation communities, and (2) determine if fire can be used as a restoration tool to enhance native plant species distribution and abundance in grasslands on the Channel Islands. Prior to burning, species composition was correlated most strongly with gradients of aspect, elevation, and the proportion of bare ground at a site. Topography was an important influence on species composition post-burn, but fire effects had a greater influence on species composition than site characteristics did during the first 2 years after the burn. Alpha diversity did not differ between burned and unburned plots, but species turnover was greater in burned plots. The response to burning varied among different vegetation guilds and within the different burn areas. Burned and unburned plots were dominated by nonnative grasses in all years, while annual forbs tended to show the greatest positive response to the burns. The richness and abundance of native species tended to either increase or remain unchanged as a result of the burns, but these effects were relatively transient. Rainfall was an important factor influencing vegetation response to the burn. Cover and species richness of annual grasses increased in wet years and probably inhibited germination and growth of most other herbaceous species. By the third year post-burn, site characteristics had a greater effect on species composition than fire effects did, and the burned plots were beginning to return to a composition similar to pre-burn conditions. If fire is to continue to be used as a restoration tool in Mediterranean-type grasslands, a better understanding of the interaction between components of fire regimes and site characteristics is needed.

*keywords:* California islands, diversity, fire, grasslands, invasive grasses, nonnative species, prescribed burns, Santa Cruz Island.

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## INTRODUCTION

The effect of biological invasions on natural systems has become an issue of worldwide concern (Drake et al. 1989, Simberloff et al. 1997, Mack et al. 2000). Although biological invasions are a natural ecological process, the worldwide rate and extent of invasions and the number of species which are now considered invasive is probably unprecedented (DiCasti 1989). Concern over the effects of invasive species has moved progressively from the local (e.g., Minnich 1980, Braithwaite et al. 1989) to regional (Macdonald et al. 1986, Naylor 1996) and even global scales (Vitousek et al. 1996, Mack and D'Antonio 1998, Mack et al. 2000).

The role of invasive species in altering fire regimes has been documented in a number of different

ecosystems (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998, Brooks 1999, D'Antonio 2000). Invasive species can change fire regimes in 2 general ways. Some species alter the distribution and composition of fuels, allowing fire to occur far more frequently in systems where historically it was an uncommon event (e.g., annual grasses [D'Antonio and Vitousek 1992, Brooks 1999]). In other ecosystems where fire was an integral natural process, invasive species can modify the scale, intensity, severity, and rates of return to such an extent that shifts in species composition and wholesale structure of communities will occur (Richardson et al. 1992). Besides these 2 general mechanisms, fire can promote invasion of nonnative species into sites that have been burned, further altering species composition and fuel characteristics which in turn modifies the fire regime (Holmes and Cowling 1997).

More traditionally though, fire has been viewed

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and used as a restoration and management tool (e.g., Biswell 1989, Parsons and Stohlgren 1989, Parsons and Swetnam 1989). There have been extensive changes in many communities as a result of fire exclusion (Parsons and Debenedetti 1979, Pyne 1984, Minnich et al. 1995), including increases in nonnative species (Hobbes and Huenneke 1992). Consequently, the restoration of fire is seen as a critical component for managing natural communities where fire was a naturally occurring process. It can also be a potential method for controlling nonnative species (Nuzzo 1991, Lonsdale and Miller 1993, DiTomaso et al. 1999). Clearly then, the contemporary role of fire must be understood from 2 different perspectives: (1) as a natural process that occurs in ecological conditions that are often drastically different from historic ones, and (2) as a restoration tool. These aspects are not necessarily exclusive, but must be evaluated by different criteria.

Grasslands in California have undergone dramatic changes in composition and distribution during the last 200 years. Community composition has been severely altered by heavy grazing from domestic livestock and the introduction of nonnative plant species, leading to a conversion from communities dominated by native perennial bunchgrasses and forbs to ones comprised predominantly of nonnative annual grasses and forbs (Heady 1977, Bartolome et al. 1986, Mack 1989). Removing grazing pressure does not lead to a return of native perennial bunchgrasses or a reduction in abundance of nonnative grasses, so nonnative herbaceous species persist in grasslands throughout the state (White 1967, Bartolome and Gemmill 1981, Baker 1989). Compounding the problems of drastically altered grazing regimes and the influx of nonnative species has been the reduction in extent of native grasslands. Since the middle of the 20th century, urbanization and agriculture have drastically reduced the amount of natural grassland area in the state. As a result of the combination of conversion from perennial to annual grassland and habitat loss, remnant patches of native perennial grassland usually exist now as small, isolated fragments.

Prescribed burning has been suggested as a potential tool for restoring native species to grassland communities and has been tested in several areas of California (Parsons and Stohlgren 1989, Menke 1992, Dyer et al. 1996, Pollak and Kan 1998, Meyer and Schiffman 1999). The results of these experiments have been mixed. In the foothills of the Sierra Nevada the biomass of nonnative annual grass was reduced and the biomass of both nonnative and native forbs increased following 3 successive burns (fall or spring), but these effects were transient and were not sustained beyond the burning treatments (Parsons and Stohlgren 1989). At Jepson Prairie in the central valley, Dyer et al. (1996) found that recruitment of the native perennial bunchgrass *Nassella pulchra* was relatively high in burned areas, but that recruitment was also dependent on variations in annual climatic conditions. Pollak and Kan (1998) reported that cover of native grass and forb species and nonnative forbs increased and that nonnative annual grass and "thatch" (organic litter)

decreased in the year after a late spring burn at Jepson Prairie. Meyer and Schiffman (1999) found that the cover of native herbaceous plants at the Carrizo Plain was greater in areas where fire had been applied in either the fall or late spring than in unburned areas or sites that had been burned in the winter. Hatch et al. (1999) reported that the native perennial bunchgrass *Danthonia californica* did not respond to fire treatments, while the response of 2 species of *Nassella* (*N. pulchra* and *N. lepida*) varied inconsistently with position along an elevation gradient.

Grassland communities on the California islands have undergone a similar conversion as the mainland due to severe overgrazing from feral and domestic livestock (Minnich 1980, Junak et al. 1995). The islands remain relatively undeveloped and loss of habitat has not been a serious problem, but habitat conversion as a result of overgrazing by feral and domestic animals has been extensive (Minnich 1980). Nonnative grass and forb species now dominate communities with herbaceous understories (grassland, oak woodlands, coastal scrub), resulting in the distribution and abundance of native herbaceous species becoming more restricted than nonnative species (Klinger 1998). Programs to remove feral and domestic animals have been undertaken by most of the organizations managing the islands (Schuyler 1993, Halvorson 1994, Keegan et al. 1994), with the primary goal of enhancing and/or restoring the composition, structure, and function of the natural communities. However, the animal removal programs will not lead to a decrease in nonnative plant species (Klinger et al. 1994, Laughrin et al. 1994). In all likelihood feral animal removal will be only a first step in a much longer management process, and other types of restoration programs will need to be tested and evaluated before an effective vegetation management protocol can be designed and fully implemented.

The historic role of fire on the structure and composition of plant communities on the California islands is poorly understood. Although it is generally accepted that fire was an important component of the islands' natural systems, and plant species on the islands have similar adaptations to fire as those on the mainland (Carroll et al. 1993), detailed information on the historic fire regime is lacking. Fire was suppressed during the last 150 years, both by human choice and lack of extensive fuels due to the severe overgrazing which had occurred. Little is known about aboriginal burning on the islands and less about naturally occurring fires, although preliminary evidence indicates that fires occurred as frequently on Santa Cruz Island as on the mainland (P. Brown, Arizona Tree Ring Laboratory, personal communication). Nevertheless, it is likely that both intentional and unintentional fires on the islands will become more frequent. They result from a continuing increase in the extent and density of fuels, natural and accidental ignition (Carroll et al. 1993), prescribed burning, and reduced suppression efforts (Wells 1991).

During this study, we used prescribed burning as an initial step in understanding the role of fire on the

structure, diversity, and composition of vegetation communities on Santa Cruz Island, and to evaluate the effectiveness of prescribed burning for creating or maintaining conditions beneficial to native species in these communities. We chose to conduct the initial studies in grasslands because of their extensive distribution on the islands, because nonnative species have had the greatest relative impact in these as opposed to other communities, and because the light, flashy fuels make grasslands the most likely areas for a fire to either start or be carried across a large part of the island. We tested 4 null hypotheses:

- (1) There would be no difference in overall species diversity between burned and unburned plots.
- (2) There would be no difference in species richness or cover of native herbaceous species between burned and unburned plots.
- (3) There would be no difference in species richness or cover of invasive nonnative herbaceous species between burned and unburned plots.
- (4) There would be no difference in fire effects as a result of variation in weather or topography.

We expected to see an increase in overall diversity in burned plots. We also expected an increase in richness and cover of native species, as well as a small reduction or no change in richness and cover of nonnative species. We felt it was likely that we would find variable responses to burning as a result of variation in weather, but believed topographic effects would not have a major influence on post-fire patterns.

## STUDY AREA

The study was conducted in grasslands on the southwest side of Santa Cruz Island. A detailed description of the island is given in Junak et al. (1995). Soils in the southwest grasslands are derived mainly from shale and silt deposits and are cut with deep gullies as a result of locally severe erosion. Three relatively broad watercourses drain the area: Poso, Alegria, and Sauces creeks. The elevation ranges from 0 to 350 m, with the topography characterized by relatively steep hills (30–80% slope) dissected by numerous small drainages.

Grassland and coastal scrub were the 2 most common plant communities that occurred in the study area. More than 80% of the area comprised grasslands, which were dominated by nonnative annual grasses (*Avena barbata*, *A. fatua*, *Bromus diandrus*, *B. hordeaceus*, *B. madritensis* ssp. *rubens*, *Lolium multiflorum*, *Vulpia myuros*), with an interspersed of native shrubs (*Artemisia californica*, *Baccharis pilularis*, *Hazardia squarrosus*, *Rhus integrifolia*). Native shrubs, nonnative grasses, and a combination of native and nonnative forbs (*Atriplex semibaccata*, *Dichelostemma capitatum*, *Erodium* spp., *Sanicula arguta*, *Sisyrinchium bellum*) dominated coastal scrub. Relatively small patches of native grass (*Nassella pulchra*) occurred throughout the grasslands and coastal scrub communities.

Table 1. Sizes and timing of prescribed burns for 1 control and 3 treatment areas in grasslands on the southwest side of Santa Cruz Island, California, 1993–1995.

Area	Size (ha)	Burn date
Control	160	Unburned
Poso	340	November 1993
Alegria	270	December 1994
Sauces	490	November 1995

## METHODS

### Data Collection

The study was conducted from the spring of 1993 to the spring of 1998. Three contiguous treatment units of varying size and configuration were randomly selected from a pool of 6 potential units to be burned. An adjacent unburned unit was selected to be an unburned control (Table 1). One of the 3 treatment units was burned each fall (early Nov–early Dec) from 1993 to 1995.

The effect of fire on herbaceous and woody species was monitored by sampling in the spring preceding each burn and then each spring for 3 years after. Data on species richness, cover of herbaceous and woody species, and density of woody species were collected in 10 burned and 10 control grassland plots (matched by year) for each of the treatments. The aspect, slope (degrees), and elevation for each plot were also recorded. Cover was estimated with the point–intercept method (Halvorson et al. 1988, Bonham 1989). A 30-m long tape was extended along a randomly selected compass bearing, and every 3 cm along the tape a thin metal rod was vertically lowered and the species of plant which it intercepted was recorded. The height of the tallest species intercepted by the point was also recorded. We made a list of all species occurring in a 2-m wide belt (1 m on either side of the tape) along the tape, and counted the number of shrubs and trees rooted within the 2-m wide belt. Shrubs were recorded if they were more than half rooted within the belt, and each species was recorded as either a seedling (no lignification of the main stem) or adult.

### Data Analysis

Three indices of alpha diversity (local or within-plot diversity) and 1 index of species turnover (across years) were calculated for each plot and for each burned and unburned area. Species richness (S) in the plots was measured as the presence of all species within the 30-m  $\times$  2-m belt, while species richness for the entire area was calculated from an incidence-based coverage estimator (ICE; Colwell and Coddington 1994). Species diversity was estimated with N2 (1/C, where C = Simpson's concentration of dominance index; Hill 1973), and species evenness was estimated using Molinari's index (E; Molinari 1989). Whitaker's index of beta diversity (W; Pielou 1975) was used to estimate species turnover. Different indices were used because a single number cannot represent species di-



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versity, and different indices convey different types of information (Magurran 1988). *S* is a fundamental measure of the number of species in a local area and is useful at small scales (e.g., a plot) where a total count of all species is feasible. However, *S* underestimates species richness on larger scales where total counts are not feasible, so other indices are needed for larger areas (Colwell and Coddington 1994). An incidence-based coverage estimator is a modification of procedures used for estimating population size of animals, and uses the presence-absence (incidence) of rare species to estimate the probability of the number of species not found in a series of samples (Colwell and Coddington 1994, Lee and Chao 1994). This estimate is added to the number of species that were recorded in the samples, and the total is used as a measure of *S*. The software application EstimateS (Colwell 1997) was used to calculate ICE, and *S*, *N*<sub>2</sub>, *E*, and *W* were calculated with program BIODIV (Baev and Penev 1995).

Differences in vegetation structure between burned and unburned plots were analyzed with Principal Components Analysis (PCA). Two analyses were conducted: 1 for pre-burn conditions using 13 variables, and 1 for pre-burn and post-burn conditions using 10 variables. The rationale for using 2 separate PCAs was to determine if the pretreatment plots assigned to burned and unburned conditions differed in structure prior to treatment. However, since elevation, aspect, and slope are physical variables that are not changed by burning, it would not make sense to include them in analyses of post-burn conditions. The 10 variables used in the second analysis maintained consistency in the structure of the correlation matrix used for PCA in the pre-burn and post-burn years. The variables used in the first PCA were the percent cover of bare ground, litter, grass, forbs, and shrubs, the total number of species in a plot (*S*), the density of shrubs, the mean height of grasses, forbs, and shrubs, and the elevation, aspect, and slope. Elevation, aspect, and slope were not included in the second analysis.

Aspect was expressed as the number of degrees from true north ( $\pm 0$ –180 degrees) and slope was measured in degrees. Cover values were arcsine transformed; height variables and shrub density were  $\log_{10} + 1$  transformed. The first 3 principal components were retained for each analysis. Differences in the values of the 3 components between burned and unburned plots were analyzed with multivariate analysis of variance (MANOVA). Because component loadings differed between years in the analysis using only the 10 vegetation variables, each year was analyzed separately (1 year pre-burn and 3 separate post-burn years).

Vegetation species were grouped into 8 different guilds (Table 2). For each guild the absolute and relative percent cover, and the mean number and percentage of species/plot were calculated. Analysis of covariance with repeated measures (RMANCOVA) was used to analyze differences in the diversity indices, cover estimates, and number and percentage of species in each guild among burn condition (burned vs. unburned) and the number of years post-burn (the

Table 2. Vegetation guilds and the number of species/guild in grassland burn areas on the southwest side of Santa Cruz Island, California, 1993–1998.

Guild	Number of species
Native annual forbs	51
Native perennial forbs	31
Native annual grass	3
Native perennial grass	5
Nonnative annual forbs	23
Nonnative perennial forbs	2
Nonnative annual grass	13
Shrubs <sup>a</sup>	12
Total	150

<sup>a</sup> There was only 1 species of nonnative shrub (*Marrubium vulgare*), so it was lumped with the other shrubs.

repeated factor). One-way nested analysis of variance (ANOVA) was used to analyze differences between burned and unburned plots for any of the variables prior to treatment (pre-burn conditions). If there were no significant differences, then the pre-burn year (YPB0) was used as a covariate in the RMANCOVA. Before using YPB0 as a covariate, the homogeneity of slope assumption of ANCOVA was analyzed with linear regression between burned and unburned plots of YPB0 on the 3 post-burn years (YPB1–YPB3). The assumption of homogeneity of slope was met for all variables.

The overall RMANCOVA for each variable was evaluated with Wilks' Lambda. If the overall analysis was significant, differences between burned and unburned conditions for the pre-burn and each post-burn year were tested with single-degree of freedom contrasts. Scatterplots and normal probability plots were used for evaluating residuals from the univariate tests to determine whether the assumptions of normality, linearity, equal variances and no outliers were valid. Cover values and the percentage of species in each guild were arcsine transformed, and a square root + 0.5 transformation was used for the absolute number of species in each guild. There were no serious violations of the univariate assumptions of RMANCOVA, so multivariate normality and equivalence of within-group variance-covariance matrices were assumed to be met. Statistical analyses for native annual grass and nonnative perennial forbs were not done because there were too few species ( $n = 3$  and 2, respectively) and they occurred in too few plots for meaningful tests.

The relationship between the number of species and the area (km<sup>2</sup>) of each burn unit was analyzed by regression of  $\log(\text{ICE})$  on  $\log(\text{area})$  (Rosenzweig 1995). The relationship between rainfall and the cover estimates and number and percentage of species in each guild were analyzed with Pearson correlation tests.

Linear regression was used to analyze the relationship between mean annual change in cover/species and cover of each species in the pretreatment conditions. Annual change was calculated for each species in burned and unburned conditions as  $\ln((C_{y_i} + 0.1)/(C_{y-1i} + 0.1))$ , where  $C$  = percent absolute cover,  $i$  = treatment condition (burned or unburned), and  $y = 0$

... 3 (0 = pre-burn, 1–3 = years post-burn). A value of 0.1 was added to all cover values to adjust for species that were not recorded within a treatment in 1 year but were recorded in either the year before or after. The independent variable in the analysis was the natural log (ln) of absolute cover (%) in pretreatment conditions.

Canonical Correspondence Analysis (CCA) was used to analyze the influence of various environmental variables on species composition between burned and unburned plots (ter Braak 1995). Variables used to test against the ordination scores included the percent bare ground and litter, slope (degrees), aspect (calculated as degrees from true north), elevation, and whether a plot was burned or not. We broke the analyses into 4 separate years: pre-burn (YPB0) and each of the 3 post-burn years (YPB1–YPB3). Because rainfall varied between years, we included each year as a covariate in the ordination, thereby adjusting the scores and holding the effect of precipitation constant. All species were included in the analysis, but we downweighted rare ones (ter Braak 1995). Randomization tests were used to test for the significance of the ordination scores for the first canonical axis and the entire ordination (ter Braak 1995).

All parametric statistical analyses were done using the GLM procedure of SYSTAT (SYSTAT 1998). Program CANOCO was used for the CCA (ter Braak and Smilauer 1998). Statistical tests were considered significant at  $P < 0.05$ , and marginally significant at  $0.05 < P < 0.10$ . Nomenclature followed Junak et al. (1995).

## RESULTS

### Vegetation Structure Patterns

The 3 principal components explained a mean of 63% of the variance in vegetation structure (Table 3). Although the magnitude of the component loadings varied between years, each component tended to represent the same gradient in structural attributes in all years (pre-burn and 3 post-burn years). The first component was a shrub gradient, the second component was a gradient from plots with relatively large amounts of bare ground to plots with continuous cover of grass, and the third component was a gradient from plots with relatively high cover of forbs to plots with high cover values of litter (Table 3). Prior to burning there was no significant difference between burned and unburned plots for any of the components in either the analysis using vegetation structure and topographic variables or the analysis using only vegetation structure variables. All 3 vegetation structure gradients were significantly different between burned and unburned plots in post-burn year 1. Burned plots had less shrub and grass cover, less litter, and more forb cover and bare ground than unburned plots (Figures 1a–c). In post-burn year 2 the shrub and litter layer gradients between burned and unburned plots continued to be significantly different, but the grass cover–bare ground gradient was not significantly different (Figure 1d). In

Table 3. Component loadings, eigen values, and percent variance accounted for by 3 principal components derived from 10 vegetation structure variables in unburned and burned grassland plots on Santa Cruz Island, California, 1993–1998. See text for explanation of variables.

Period	Variable	Principal component		
		1	2	3
Pre-burn	S	0.605	0.069	0.406
	Forb cover (%)	−0.016	−0.507	0.661
	Forb height	0.289	−0.445	0.008
	Grass cover (%)	−0.375	0.656	0.467
	Grass height	0.331	0.268	−0.389
	Shrub cover (%)	0.726	0.452	0.135
	Shrub density	0.829	0.254	0.267
	Shrub height	0.729	0.031	0.023
	Bare ground (%)	0.360	−0.751	0.132
	Litter (%)	0.473	−0.117	−0.670
Year 1 post-burn	Eigenvalue	2.80	1.81	1.53
	% Variance	28.0	18.1	15.3
	S	0.640	0.330	0.199
	Forb cover (%)	−0.037	0.076	0.746
	Forb height	0.277	0.372	−0.294
	Grass cover (%)	0.439	−0.770	0.168
	Grass height	0.636	−0.379	−0.065
	Shrub cover (%)	0.739	0.348	0.165
	Shrub density	0.706	0.381	0.256
	Shrub height	0.672	0.024	−0.383
Year 2 post-burn	Bare ground (%)	−0.346	0.642	0.442
	Litter (%)	−0.095	0.557	−0.607
	Eigenvalue	2.71	1.98	1.52
	% Variance	27.1	19.8	15.2
	S	0.543	0.448	0.277
	Forb cover (%)	−0.066	0.536	0.728
	Forb height	0.446	0.061	0.123
	Grass cover (%)	−0.570	0.683	−0.095
	Grass height	−0.471	0.591	−0.249
	Shrub cover (%)	0.655	0.458	−0.250
Year 3 post-burn	Shrub density	0.685	0.542	0.002
	Shrub height	0.697	0.155	−0.284
	Bare ground (%)	0.470	−0.407	0.611
	Litter (%)	0.646	−0.242	−0.396
	Eigenvalue	3.07	2.06	1.37
	% Variance	30.7	20.6	13.7
	S	0.750	−0.111	0.452
	Forb cover (%)	0.365	−0.248	0.568
	Forb height	0.149	0.360	−0.492
	Grass cover (%)	−0.566	0.581	0.386
Year 3 post-burn	Grass height	−0.389	0.703	0.363
	Shrub cover (%)	0.669	0.502	−0.085
	Shrub density	0.656	0.450	0.247
	Shrub height	0.661	0.453	−0.136
	Bare ground (%)	0.635	−0.405	0.076
	Litter (%)	0.318	0.157	−0.556
	Eigenvalue	3.01	1.88	1.45
	% Variance	30.1	18.8	14.5

post-burn year 3 there were significant differences in the shrub gradient and the grass cover–bare ground gradient between burned and unburned plots, but no significant difference in the gradient between forb cover and litter (Figure 1e).

### Species Diversity Patterns

There were no significant differences between burned and unburned plots in the pre-burn years for any of the diversity variables (S, N2, E, and W) or for any of the variables used to measure composition

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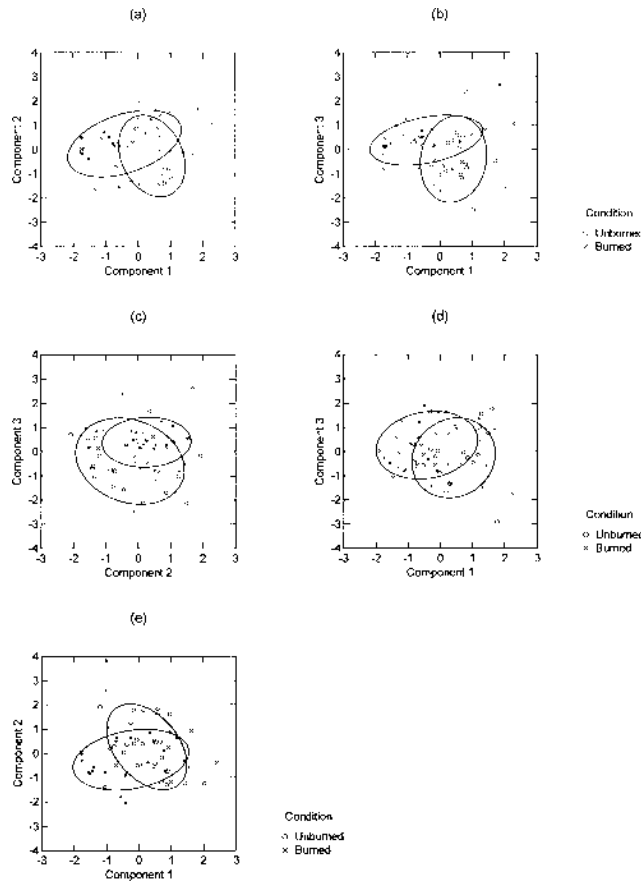


Fig. 1. 95% confidence ellipses for principal component scores of burned and unburned grassland plots on Santa Cruz Island, California, 1993–1998. Component 1 is a gradient from plots with relatively larger amounts of bare ground to plots with continuous cover of grass, and Component 3 is a gradient from plots with high cover of litter to plots with relatively high cover of forbs.

(number of species/plot, percentage of species/plot, absolute cover, and relative cover) for any of the guilds. Therefore, all analyses of diversity and composition are for the post-burn years 1–3.

There was no significant relationship between ICE and  $\log(\text{area})$  ( $r = 0.091$ ;  $df = 1, 22$ ;  $P = 0.62$ ). At the burn unit scale, there was no significant difference for S, N2, or E between burned and unburned plots; however, values for W were significantly greater in burned conditions than unburned conditions (Figure 2). There were no significant differences between burned and unburned plots for S, N2, or E, but W was significantly greater in burned plots than in unburned plots in post-burn year 1 (Figure 2). Mean species richness was 19.1 species/plot ( $SE = 0.5$ ). The mean value for N2 in the plots was 4.3 ( $SE = 0.2$ ), and for E 0.72 ( $SE = 0.01$ ).

## Guild Patterns

Species richness of annual forbs was significantly greater in burned plots during post-burn year 1 and marginally so during post-burn year 3 ( $F = 3.69$ ;  $df = 1, 53$ ;  $P = 0.06$ ; Figure 3). The absolute cover of annual forbs was significantly greater in burned plots

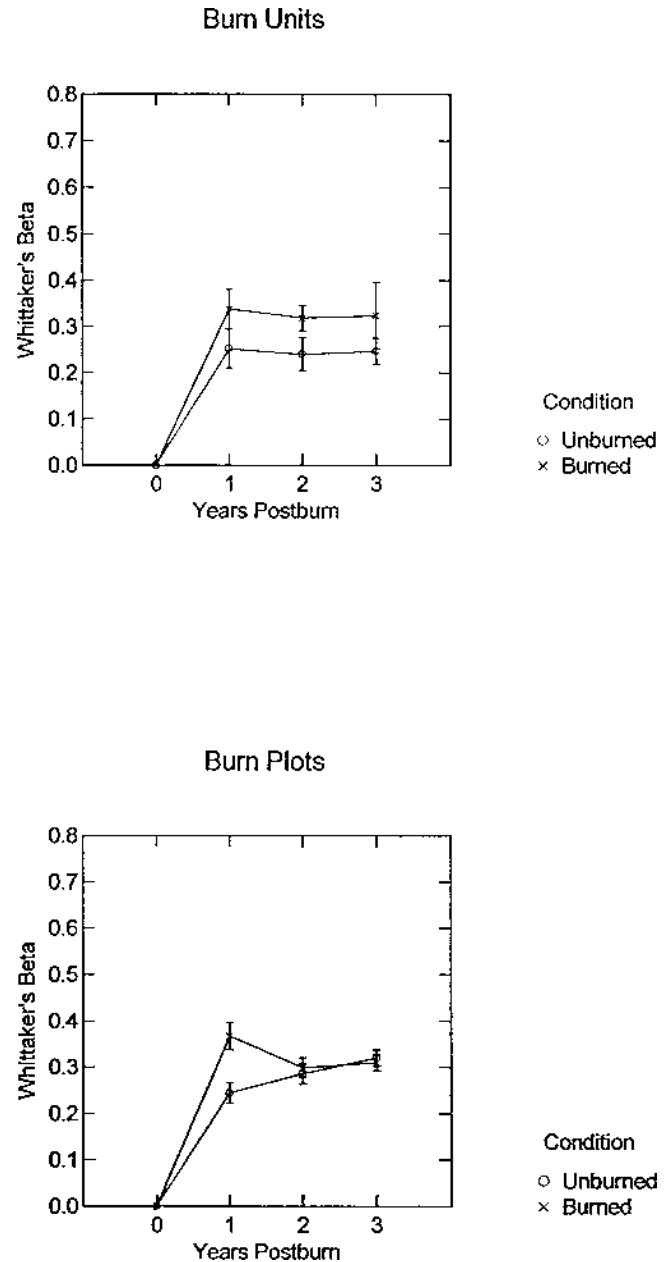


Fig. 2. Differences in species turnover between burned and unburned grassland areas on Santa Cruz Island, California, 1993–1998.

than unburned plots during post-burn years 1 and 2 (Figure 4). Annual forbs constituted 31.4–47.1% of the species in burned plots and 33.8–36.7% in unburned plots. Relative cover of annual forbs in burned plots ranged from 7.5 to 24.5% and from 8.6% to 12.3% in unburned plots.

There were significantly more native annual forb species in burned plots than unburned plots in all post-burn years (Table 4). Native annual forbs constituted 11.2% of the species in burned plots and 6.2% in unburned plots. Mean absolute cover of native annual forbs was significantly greater in burned plots than unburned plots in post-burn years 1 and 3, and marginally greater in post-burn year 2 ( $F = 2.979$ ;  $df = 1, 53$ ;  $P = 0.090$ ). The relative cover of native annual

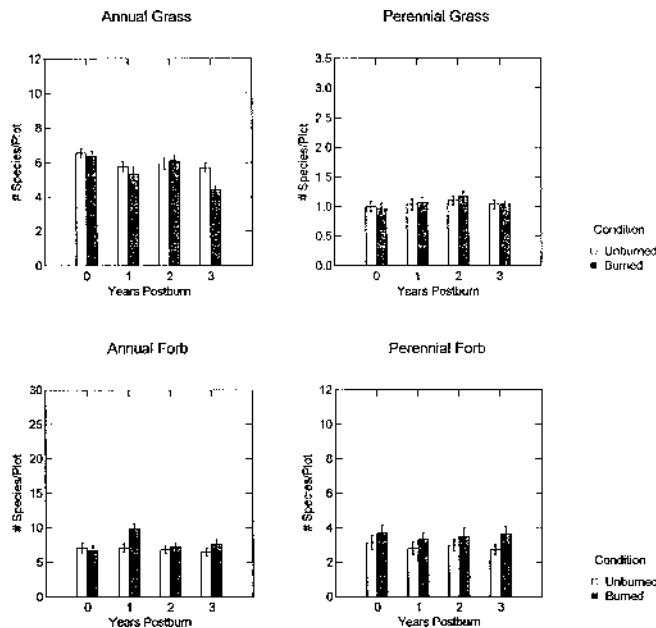


Fig. 3. Mean species richness ( $\pm 1$  SE) of 4 vegetation guilds in burned and unburned grassland plots on Santa Cruz Island, California, 1993–1998.

forbs in burned plots was 2.1% and 0.4% in unburned plots. There were no significant differences in species richness or absolute cover between burned and unburned plots for native perennial forbs (Table 4). Native perennial forbs constituted 10.3% of the species and 1.6% of the relative cover in all plots.

Significantly more nonnative annual forb species occurred in burn plots than unburned plots in post-burn year 1 (Table 4). The absolute cover of nonnative annual forb species was significantly greater in burned plots in post-burn years 1 and 2 (Table 4). Nonnative annual forbs constituted 29.8% of the species in burned and unburned plots. Relative cover was 14.8% in burned plots and 10.2% in unburned plots.

The mean number of annual grass species was significantly lower in burned plots than in unburned plots in post-burn years 1 and 3 (Figure 3). Absolute cover of annual grass decreased in burned plots post-burn year 1, but then was significantly greater in burned than unburned plots in post-burn year 2 (Figure 4). Annual grass constituted 33.3% of the species in unburned plots and 29.2% in burned plots. Relative cover of annual grass in unburned plots was 23.4% and 24.5% in burned plots.

There was no significant difference in mean absolute cover or mean number of species between burned and unburned plots for perennial grasses (Figures 3–4). The mean percentage of perennial grass species was 6.1% and mean relative cover was 9.0%. There was no significant difference in the number of perennial forb species between burned and unburned plots (Figure 3). However, absolute cover of perennial forbs in burned plots decreased from 19.3% prior to burning to a mean of 5.2% after the burns, while the absolute cover of perennial forbs in unburned plots decreased from 15.9% to 4.2% (Figure 4). The mean

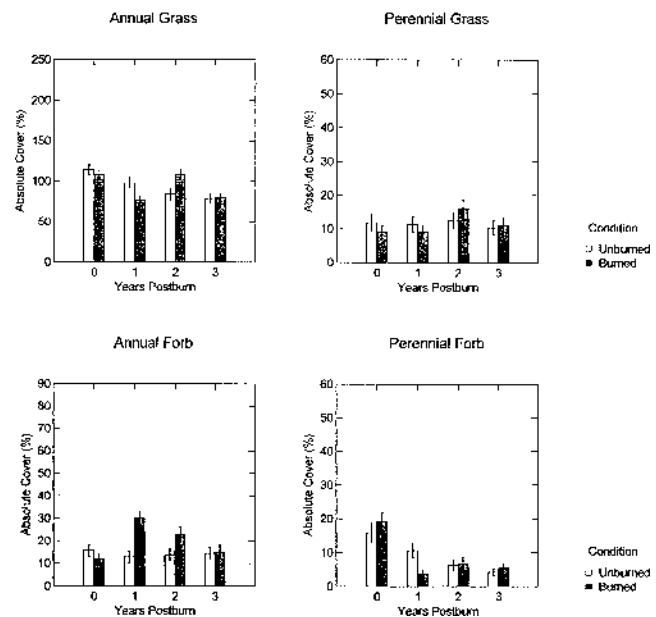


Fig. 4. Mean absolute cover ( $\pm 1$  SE) of 4 vegetation guilds in burned and unburned grassland plots on Santa Cruz Island, California, 1993–1998.

percentage of perennial forb species in all plots was 15.8%. Mean relative cover ranged from 2.9% to 5.1% in burned plots and from 4.1% to 7.6% in unburned plots.

The mean number of shrub species in burned plots was 1.3/plot and in unburned plots 2.1/plot (Wilks' Lambda = 0.837;  $F = 3.32$ ;  $df = 3, 51$ ;  $P = 0.027$ ). The absolute cover of shrubs was significantly lower in burned plots than unburned plots (Wilks' Lambda = 0.779;  $F = 4.84$ ;  $df = 3, 51$ ;  $P = 0.005$ ), but there was no significant difference in shrub density between burned and unburned plots. Mean shrub density was 16.7/plot (SE = 5.2) in burned plots and 11.7/plot (SE = 2.03) in unburned plots. Shrubs constituted 10% of the species in unburned plots and 5% in burned plots. The relative cover of shrubs ranged from 3 to 5% in unburned plots and from 1.5 to 5% in burned plots.

The absolute cover of nonnative grasses had a significant positive relationship with annual rainfall (Table 5). Twenty-five percent of the variation in cover of nonnative grass in burned areas was explained by rainfall, and 22% in unburned areas. The number of nonnative grass species in burned areas had a marginally significant positive relationship with annual rainfall (Table 5), but only 4% of the variation was explained by the relationship. Species richness of nonnative forbs in burned and unburned areas and absolute cover in unburned areas had significant negative relationships with rainfall, but the amount of variation explained by the relationships was small (3%–6%). There was no significant relationship between rainfall and species richness and cover of native herbaceous species (Table 5).

The response of the different vegetation guilds varied substantially among the different burn units. The nested factor was significant in virtually all of the statistical tests we conducted for the vegetation guilds



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Table 4. Mean (upper value) and standard error (lower value) for species richness and absolute cover (%) of 7 vegetation guilds in burned and unburned plots on Santa Cruz Island, California, 1993–1998. Years Post-burn 0 = Pre-burn conditions.

Guild	Years post-burn	Species richness		Absolute cover	
		Unburned	Burned	Unburned	Burned
Native annual forbs	0	1.90	2.20	1.7	1.9
		0.47	0.48	0.8	0.8
	1	1.57	3.63	0.8	4.5
		0.37	0.69	0.6	1.6
	2	1.40	2.37	0.8	1.7
		0.35	0.52	0.6	0.7
	3	1.30	2.47	0.3	2.5
		0.37	0.63	0.1	1.1
	0	2.13	2.67	1.7	4.4
		0.42	0.45	0.6	1.7
Native perennial forbs	1	1.83	2.47	1.5	3.0
		0.36	0.38	0.5	0.9
	2	2.00	2.60	0.9	3.9
		0.32	0.44	0.3	1.8
	3	1.83	2.57	1.0	2.4
		0.28	0.45	0.3	0.9
Native annual grass	0	0.63	0.33	1.6	0.5
		0.09	0.12	0.4	0.2
	1	0.43	0.23	1.1	0.7
		0.09	0.09	0.4	0.6
	2	0.37	0.23	0.8	0.3
		0.09	0.08	0.3	0.3
	3	0.17	0.07	0.1	0.1
		0.07	0.05	0.1	0.1
Native perennial grass	0	1.00	0.97	11.9	9.0
		0.08	0.09	2.3	1.9
	1	1.03	1.07	11.3	8.9
		0.08	0.09	2.1	1.9
	2	1.10	1.17	12.3	16.0
		0.07	0.09	2.2	2.6
	3	1.03	1.03	10.3	11.1
		0.08	0.06	2.1	2.1
Nonnative annual forbs	0	5.20	4.47	14.0	10.0
		0.35	0.39	2.4	2.0
	1	5.53	6.23	12.1	25.6
		0.38	0.28	2.3	2.6
	2	5.40	4.80	13.1	21.1
		0.36	0.25	2.2	3.1
	3	5.20	5.13	14.2	12.7
		0.35	0.31	2.6	2.2
Nonnative perennial forbs	0	1.00	1.00	14.2	14.8
		0.01	0.01	2.4	2.3
	1	0.97	0.87	9.1	0.6
		0.03	0.06	2.0	0.2
	2	0.97	0.90	5.3	2.7
		0.03	0.06	1.3	0.7
	3	0.87	1.03	3.1	3.1
		0.06	0.03	0.8	0.7
Nonnative annual grass	0	5.90	6.00	112.6	107.5
		0.19	0.27	5.7	5.5
	1	5.33	5.10	96.9	76.2
		0.25	0.36	6.5	3.9
	2	5.57	5.87	83.1	107.8
		0.27	0.26	6.5	6.3
	3	5.53	4.33	78.4	79.7
		0.27	0.26	5.3	4.7

(Table 6). In contrast, the main effect (burning) was significant in just under 66% of the tests (Table 6).

## Species Patterns

There was a significant negative relationship between the mean annual change in cover and pretreatment cover for native and nonnative forbs (Figure 5). The relationship accounted for 73% of the variation in

the mean annual rate of change for native forbs but only 19% for nonnative forbs. There was no significant difference in the slope or intercepts between burned and unburned conditions for species in either guild. There was no significant relationship between the mean annual change in cover and pretreatment cover for native or nonnative grasses.

Three canonical axes could be interpreted in each of the 4 CANOCO ordinations. The 3 axes accounted



Table 5. The correlation between rainfall and species richness and absolute cover in burned and unburned plots for 4 vegetation guilds on Santa Cruz Island, California, 1993–1998.

Guild	Variable	Treatment	Slope	R	df	P
Nonnative forbs	Species richness	Unburned	-0.027	0.168	1, 148	0.040
		Burned	-0.033	0.248	1, 88	0.018
	Absolute cover (%)	Unburned	0.350	0.240	1, 148	0.003
		Burned	0.095	0.087	1, 87	0.415
Nonnative grass	Species richness	Unburned	0.012	0.110	1, 148	0.182
		Burned	0.028	0.205	1, 88	0.053
	Absolute cover (%)	Unburned	1.270	0.470	1, 148	<0.001
		Burned	1.068	0.499	1, 86	<0.001
Native forbs	Species richness	Unburned	-0.010	0.031	1, 148	0.705
		Burned	0.011	0.032	1, 85	0.770
	Absolute cover (%) (arcsine)	Unburned	-0.001	0.050	1, 147	0.255
		Burned	0.002	0.094	1, 88	0.377
Native grass	Species richness	Unburned	0.007	0.126	1, 147	0.125
		Burned	0.007	0.129	1, 88	0.226
	Absolute cover (%) (arcsine)	Unburned	0.002	0.100	1, 148	0.245
		Burned	0.002	0.176	1, 87	0.099

for 76–83% of the variance between species composition and the environmental variables, and between 13 and 15% of the variability in the species' abundances (Table 7). All Monte Carlo tests for both the first canonical axis and the overall ordination were significant.

Species composition shifted as a result of burning, and this effect was most pronounced in post-burn year 1 (Table 7). During the pre-burn conditions, species composition was influenced most by the physical nature of the plots, specifically the aspect, elevation, and slope (Table 7 and Figure 6A). Species composition in post-burn year 1 was correlated most strongly with the burn condition of a plot (Table 7). There was a distinct separation of burned and unburned plots in post-burn year 1, and there was a strong association of the distribution and abundance of most native forb species with burn plots (Figure 6B). This pattern continued into post-burn year 2, although the relationship was not as strong as in post-burn year 1 (Table 7). The correlation of burning with the first canonical axes dropped from 0.83 to 0.45, and species composition differences between burned and unburned plots were

not as distinct (Figure 6C). By post-burn year 3, the difference in species composition between burned and unburned plots had further weakened, and species composition was related more strongly to the aspect of a plot than to burning (Table 7 and Figure 6D).

## DISCUSSION

From an ecological perspective, single fire events had only temporary effects on species composition and structure of grasslands on Santa Cruz Island. There were differences between burned and unburned conditions for some of the variables we measured, but, in general, the effects were brief and limited to post-burn year 1, and, to a lesser extent, post-burn year 2. These differences were often inconsistent among years, treatments, and burn area as well. These outcomes are similar to what Dyer et al. (1996) found in grasslands at Jepson Prairie and Hatch et al. (1999) found in coastal prairie grasslands. In both of these studies the regeneration of native bunch grass was as dependent on environmental variation as it was on burning or grazing treatments.

The effect of fire on species diversity was relatively minor. Alpha diversity (*S*, *N*<sub>2</sub>, and *E*) did not differ between burned and unburned plots or the larger units the plots were nested within, although the small

Table 6. The number of analysis of covariance with repeated measures statistical tests with significant nested and main effects for 6 vegetation guilds in burned and unburned grassland plots on Santa Cruz Island, California, 1993–1998. ns = not significant, + = significant.

Guild	Variable	Nested effect	Main effect
Nonnative annual forb	Species richness	+	+
	Absolute cover (%)	+	+
Nonnative grass	Species richness	+	+
	Absolute cover (%)	+	+
Native annual forb	Species richness	+	+
	Absolute cover (%)	+	+
Native perennial forb	Species richness	+	ns
	Absolute cover (%)	+	ns
Native grass	Species richness	+	ns
	Absolute cover (%)	ns	ns
Shrubs	Species richness	+	+
	Absolute cover (%)	+	+
	Density	+	ns

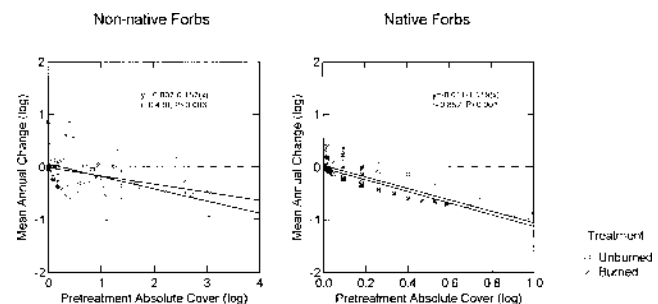


Fig. 5. The relationship between absolute cover prior to burning treatments and the change in cover relative to pretreatment conditions for species in grasslands on Santa Cruz Island, California, 1993–1998.

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Table 7. Variable loadings and percent of variance accounted for 3 axes derived by canonical correspondence analysis of 150 plant species in burned and unburned grasslands on the southwest side of Santa Cruz Island, California, 1993–1998.

Variable	Species axis			Environmental axis			Axes			
	1	2	3	1	2	3	Summary	1	2	3
Pre-burn										
Bare ground (%)	−0.018	0.652	0.159	−0.023	0.953	0.228	Eigenvalue	0.120	0.069	0.060
Litter (%)	0.394	0.146	−0.093	0.489	0.213	−0.134	Species/environment	0.806	0.685	0.698
Burned	0.217	0.086	−0.605	0.269	0.125	−0.866	Cumulative % species	7.2	11.4	15.0
Aspect	−0.629	0.093	−0.200	−0.781	0.136	−0.287	Cumulative % species/environment	39.8	62.7	82.7
Slope	−0.353	0.123	0.133	−0.438	0.180	0.190				
Elevation	−0.437	−0.019	0.418	−0.542	−0.028	0.599				
Year 1 post-burn										
Bare ground (%)	0.393	−0.076	0.148	0.454	−0.094	0.267	Eigenvalue	0.128	0.107	0.058
Litter (%)	0.031	0.536	0.263	0.036	0.667	0.475	Species/environment	0.866	0.804	0.553
Burned	0.826	−0.139	0.035	0.954	−0.173	0.064	Cumulative % species	6.6	12.1	15.1
Aspect	−0.281	−0.516	0.297	−0.324	−0.642	0.537	Cumulative % species/environment	33.5	61.5	76.6
Slope	−0.277	−0.262	−0.119	−0.320	−0.326	−0.216				
Elevation	−0.535	−0.110	0.120	−0.617	−0.137	0.217				
Year 2 post-burn										
Bare ground (%)	0.152	−0.095	0.273	0.227	−0.128	0.419	Eigenvalue	0.109	0.106	0.076
Litter (%)	0.097	−0.167	0.507	0.146	−0.226	0.778	Species/environment	0.663	0.737	0.652
Burned	0.450	0.352	−0.271	0.679	0.478	−0.416	Cumulative % species	4.9	9.6	13.0
Aspect	0.225	−0.642	−0.137	0.339	−0.871	−0.210	Cumulative % species/environment	29.0	57.2	77.4
Slope	−0.275	−0.243	−0.055	−0.415	−0.329	−0.084				
Elevation	−0.281	−0.346	0.131	−0.424	−0.469	0.201				
Year 3 post-burn										
Bare ground (%)	0.237	0.350	0.120	0.337	0.571	0.219	Eigenvalue	0.152	0.086	0.062
Litter (%)	0.023	0.136	0.348	0.033	0.222	0.636	Species/environment	0.703	0.614	0.547
Burned	−0.319	0.384	−0.222	−0.454	0.626	−0.405	Cumulative % species	6.9	10.7	13.5
Aspect	0.646	−0.022	−0.161	0.919	−0.036	−0.295	Cumulative % species/environment	38.6	60.5	76.2
Slope	0.044	−0.062	−0.106	0.063	−0.101	−0.194				
Elevation	0.139	−0.137	−0.107	0.197	−0.223	−0.195				

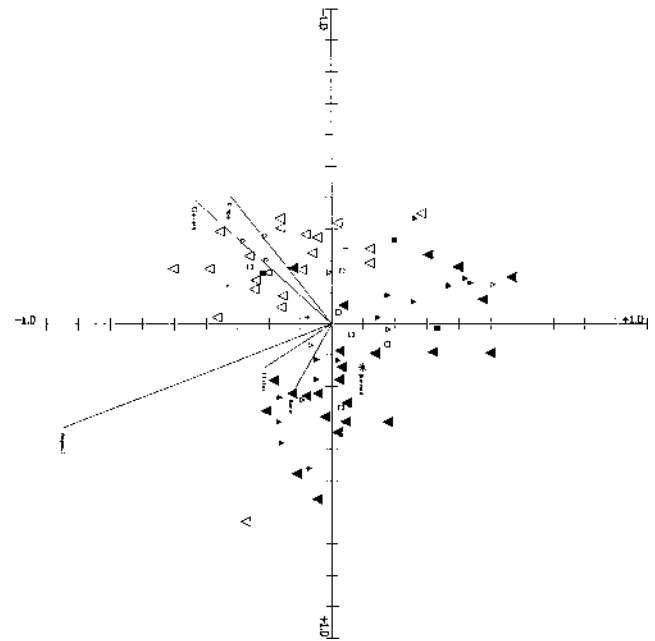


Fig. 6C. Canonical Correspondence Analysis triplot of site and species scores for grassland plots on Santa Cruz Island, California. Symbols: large upside-down dark triangles = burned plots; large upside-down open triangles = unburned plots; small dark triangles = native forbs; small open triangles = nonnative forbs; small dark squares = native grass; small open squares = nonnative grass; crosses = shrubs. Data are for post-burn year 2.

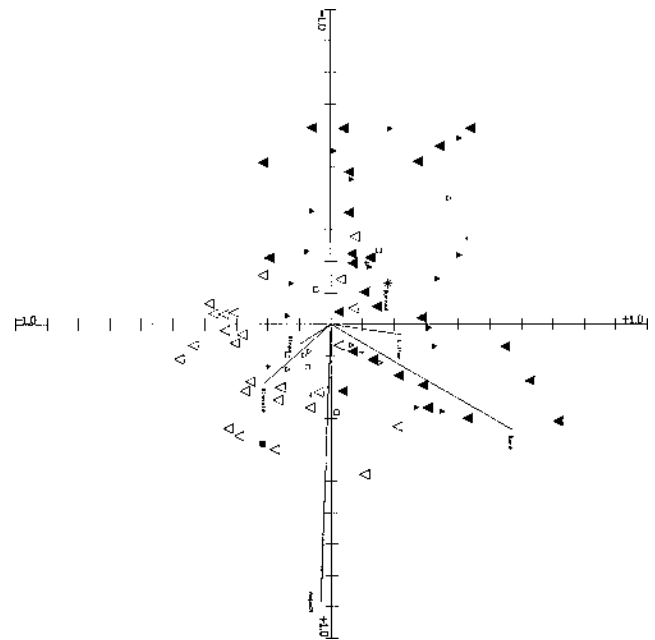


Fig. 6D. Canonical Correspondence Analysis triplot of site and species scores for grassland plots on Santa Cruz Island, California. Symbols: large upside-down dark triangles = burned plots; large upside-down open triangles = unburned plots; small dark triangles = native forbs; small open triangles = nonnative forbs; small dark squares = native grass; small open squares = nonnative grass; crosses = shrubs. Data are for post-burn year 3.

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sample size at the larger scale ( $n = 6$ ) made statistical power low. The differences in species turnover between burned and unburned plots in post-burn year 1 was most likely due to increased germination by fire-following species. At the burn unit scale species turnover was greater in burned areas than unburned areas in all years. The greater turnover of species detected at the scale of the burn units in post-burn years 2 and 3 and not in the plots was probably because many species occurred at low abundance or patchily within the unit. The response of these species to the burns could not be detected in the plots, whereas it could at the larger scale of the burn unit.

Burning had predictable but short-term effects on vegetation structure in the grasslands. There was less litter and shrub cover and more bare ground after the burn, but annual grasses dominated the cover in both burned and unburned conditions in all years. By post-burn year 3 the cover of annual grass and litter was similar in burned and unburned plots. Shrub cover and height were reduced in burned areas, but shrub density did not change greatly. Although it may seem contradictory for shrub density not to change while cover decreases, this is because the dominant shrub species occurring in the burned areas on Santa Cruz have the capability to both resprout and regenerate from seed. Therefore, although cover was reduced because leaves and stems were burned back, relatively few of the shrubs died, and density remained about the same.

Topography and rainfall were the primary factors determining species composition in unburned conditions in grasslands on Santa Cruz Island. Fire had stronger effects on species composition than topography in post-burn years 1 and 2. But the fire effects were transient, and by post-burn year 3, they had ceased to be as important as topographic characteristics. Differences in annual rainfall had an important effect on some guilds, especially annual grasses. Although there was no correlation between rainfall and cover or species richness of native species, this does not imply native herbaceous species do not respond to rainfall after a fire. Because annual grasses had a strong positive response to rainfall they probably suppressed germination and growth of native herbaceous species, as well as nonnative forb species. In areas where annual grasses are not as abundant as in grasslands on Santa Cruz Island it is likely that there would be a stronger positive relationship between rainfall and herbaceous species other than annual grasses.

Annual forbs, especially native annual species, tended to show a relatively consistent positive response to the burns, and the cover of annual grass was reduced in post-burn year 1. Parsons and Stohlgren (1989) reported a similar pattern in grasslands in the foothills of the Sierra Nevada, and this pattern has been well recognized for years in other communities in Mediterranean climates (Trabaud 1994). On Santa Cruz Island different guilds showed different temporal patterns for species richness and abundance in the burned areas, but again, by post-burn year 3, virtually all guilds in the burned areas were returning to the

same relative levels of abundance as in unburned areas.

Fire ecologists have become increasingly aware that many factors interact to influence fire effects on species composition. These include the season a burn occurs, fire behavior (intensity, rate of spread, severity), the spatial and temporal scales associated with the fire regime, landscape level processes, and historical land use (Naveh 1994, Whelan 1995). Besides topography and rainfall, it is very possible that other factors, such as soil conditions and fire behavior, had important influences on species composition in burned grasslands on the island as well. Historically, all of the areas had different levels of grazing by feral sheep and livestock, which resulted in variable amounts of bare ground both between and within the burn units. This likely had indirect influence on fire effects by modifying fire behavior at local scales (intensity and duration), site scales (intensity, duration, extent, type), and landscape scales (intensity, duration, extent, type, seasonality, frequency).

Some studies indicate post-fire vegetation changes occur during a brief period of time (Holland 1986) and are characterized mainly by species already occurring within the burn area. Relative abundance can change, but the basic suite of species does not ("autosuccessional;" Hane 1971). Our data support this concept, and it is unlikely that diversity patterns would change in any systematic way under these conditions. Furthermore, because annual grasses produce rich seed banks, it is unlikely that a single fire would deplete these. Studies in grasslands throughout California have shown that annual grass continues to remain the most abundant group of plants after a burn (Parsons and Stohlgren 1989, Dyer and Rice 1997, Pollak and Kan 1998, Meyer and Schiffman 1999).

Several caveats to this study need to be mentioned. Although we had multiple burn units, the burns were not spatially replicated within years. Burning in multiple years gave us a chance to analyze responses under varying environmental conditions (e.g., rainfall), but the lack of replication within years probably confounded, at least to a certain degree, differences among fire effects, site characteristics, and variation in rainfall. The pre-burn composition and structure of the vegetation was very similar between the sites, but spatial replication would have effectively partitioned site and temporal variability. In addition, because there were only 3 burn units and they had variable responses to the fire (the nested effect), our statistical power was low in a number of our analyses. Finally, we did not have adequate data on fire behavior at the plot scale, and it is well known that variation in fire behavior can lead to different vegetation responses at local scales (Vogl 1974).

From a restoration perspective, single fires on Santa Cruz Island had relatively little effect in enhancing grassland communities for native species. But the results were not entirely discouraging because species richness and cover of native species temporarily increased or remained unchanged. Nonnative annual species continued to dominate burned areas in our



study, but richness and cover of these species did not increase. The grasslands on Santa Cruz Island are very similar to those in the interior valley and foothill areas of California, where species composition has been drastically altered by grazing and the abundance of nonnative annual grasses (Heady 1977, Dyer and Rice 1997), so the patterns we observed are likely to be representative of many sites on the mainland (e.g., Parsons and Stohlgren 1989). However, because our study only involved single burns done in the fall, generalizing about fire effects beyond this type of burn would be inappropriate. Still, it is clear it will be necessary to significantly modify species composition at both local and site scales before native species can begin to reach levels of abundance comparable to that of nonnative species (Dyer and Rice 1997), and single fires done in the fall will not be effective at this.

Alternatives to single fall burns include changing the season during which burns are conducted and/or the frequency with which they are conducted. The cover and richness of native herbaceous species has been reported to be greater after spring burns than fall burns (Pollak and Kan 1998, Meyer and Schiffman 1999), and a positive response by native herbaceous species was associated with burning in successive years to control *Centaurea solstitialis* (DiTomaso et al. 1999). It is important to recognize most of these have been short-term studies (2–3 years) and limited in geographic extent, but the results are encouraging and indicate that, at least in some local situations, fire can have positive effects for native species. But developing an effective management burning regime will be difficult, because, as Hatch et al. (1999) observed, 1 particular fire regime that is beneficial to 1 species or group of species may not be beneficial to other equally desirable species.

As Whelan (1995) pointed out, if conservation of biodiversity is the primary management goal, trying to determine and mimic a historical fire regime may be inappropriate. Developing a prescribed burning regime that is beneficial to native species in grasslands in California will take years of experimentation and evaluation at different scales. An important step in this process will be to determine which components of a fire regime can be manipulated to benefit the most native species, and then to determine the range of environmental conditions under which these can then be applied (Kilgore 1973). The ecosystem that the historic fire regime on Santa Cruz Island occurred in has been significantly altered, and it is unrealistic to expect desired outcomes to occur quickly under the present conditions. This situation applies to many mainland areas as well. Management burns and wildfires are both single-time events, and our study is likely representative of how conditions at a particular point in time will determine burn effects and how variable the responses will be. But to partition site variation from temporal variation, it will be critical to conduct studies that are blocked spatially and temporally. This may not be practical at large scales, but the use of small-scale experiments where different components of the fire regime (e.g., season, frequency, and return interval) are

manipulated (e.g., Meyer and Schiffman 1999) across varying gradients would be timely and lead to better understanding of variation in fire effects. These findings could then be applied to relatively large areas where the influence of larger landscape level factors (topography, climate, environmental patchiness, fire duration, extent, intensity) on the management prescription could be evaluated. Incorporating longer time scales into studies on fire in grasslands in California should also be encouraged. Presumably because fire effects on vegetation in grasslands are relatively short-term, there have been few published studies that extend beyond 2–3 years. But as different components of fire regimes are manipulated, it will be important to extend our perspective beyond the narrow time frame typical of most studies.

## CONCLUSIONS

As more and more areas become impacted and altered by invasive plants and animals, it will be important for scientists and land managers to evaluate these impacts from both an ecological and a conservation perspective. It is recognized that the invasion of nonnative species can alter disturbance regimes, often leading to patterns of succession and composition in the disturbed communities that differ from historic ones (Mack and D'Antonio 1998). The interaction between fire and invasive species may be an important process contributing to global changes, but from an ecological perspective it does not make sense to ask whether fire belongs in a particular system or not, and this bias needs to be avoided. If fire is occurring in an ecosystem, then the conditions to support fire already exist and fire will continue to occur. What is important ecologically is to study the interaction between fire and invasive species along gradients that influence distribution and abundance patterns, and to develop a better understanding how fire effects vary along those gradients.

From a conservation perspective, it is appropriate to ask how fire should be managed in particular ecosystems. The decision of whether to exclude fire from particular systems or, alternatively, how to use it as a restoration and management tool, must be based on an understanding of the range of ecological effects that fire produces. Few truly natural systems exist anymore, and, for agencies responsible for managing natural communities and their resources, determining what the outcomes will be of a natural process within the context of ecosystems severely altered in composition and structure will be a very important undertaking.

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